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REVISED GENERIC DIAGNOSES OF THE FOSSIL FISHES MEGALICHTHYS AND ECTOSTEORHACHIS (FAMILY OSTEOLEPIDAE).

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With One Plate

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No. 9 — *Revised generic diagnoses of the fossil fishes* Megalichthys *and* Ectosteorhachis (*family Osteolepidae*).

By Keith Stewart Thomson[1]

In the course of studies on the morphology of the Rhipidistia (fossil fishes of the order Crossopterygii) I have found it necessary to enquire into the systematics of certain of the forms concerned, notably *Ectosteorhachis* and *Megalichthys* (members of the family Osteolepidae).

The name *Ectosteorhachis* was coined by Cope (1880) for material of a rhipidistian collected in the Permian "red-beds" of Texas. Cope described the type species, *Ectosteorhachis nitidus*, and later (1883) a second species, *E. ciceroneus*, which he differentiated from *E. nitidus* by the nature of the surface ornamentation of the dermal bones of the skull. Hussakof (1911) showed that the two forms actually belong to the same species. Until recently remains of *Ectosteorhachis* were rare, but now a considerable amount of material, particularly in the collections of the Museum of Comparative Zoology, is available for study. *Ectosteorhachis* has only been found in the Lower Permian of the United States, and the principal collections have been made in the Wichita Group (Moran to Belle Plains formations); a single jaw in the Museum of Comparative Zoology was recently collected in the Dunkard Group, Lower Permian, of Clarke Hill, Ohio.

In 1891 Cope decided that his genus *Ectosteorhachis* was indistinguishable from the form known as "*Megalichthys*" — a common Carboniferous genus well known in the European Coal Measures. In more recent times re-study of *Ectosteorhachis*, as Romer (1941) has noted, has led to the suggestion that this form is, after all, a distinct genus. The aim of this paper is to explore this view, by a comparative anatomical study of the two forms; as will be seen, the conclusion reached is that *Ectosteorhachis* should be re-established as a valid genus.

"*Megalichthys*" is a rhipidistian occurring very commonly in the Carboniferous deposits of Europe, where it is frequently found in the ironstone shales associated with workable coal seams, and less commonly in the Carboniferous of North America. Unfortunately, there is considerable confusion concerning the

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nomenclature of this genus and at the end of this paper I have included a discussion of this problem. The name *Megalichthys* throughout this study is used in the sense of Smith-Woodward (1891) as is, in fact, the common usage of the name.

Several species of *Megalichthys* have been described; the discussion of the genus given below is based mainly on the structure of the type species *Megalichthys hibberti* Agassiz. *Megalichthys coccolepis* Young, *intermedius* Woodward, *laticeps* Traquair, and *macropoma* Cope, have been distinguished from *M. hibberti* principally on the relative proportions of the maxillae and gular plates and such distinctions do not affect our present discussion in any way.

During this study, which formed part of my dissertation for the degree of Doctor of Philosophy at Harvard University, I have been greatly assisted by Professor A. S. Romer. I am also grateful to him for the use of the collections and facilities of the Museum of Comparative Zoology. I am indebted to Professor G. G. Simpson for his criticism of the final section of this paper. I must also thank Dr. E. I. White, Keeper of Palaeontology at the British Museum (Natural History), London, who allowed me to spend several weeks studying in his department during the summer of 1962. Mr. H. A. Toombs of the British Museum (Natural History) and Dr. C. D. Waterston of the Royal Scottish Museum, Edinburgh, have also given me assistance and advice; I am particularly grateful to the latter for his efforts to identify for me various specimens from the Hibbert Collection in the Royal Scottish Museum.

Dr. B. Schaeffer of the American Museum of Natural History, Dr. D. Baird of Princeton University, and Dr. P. P. Vaughn of the University of California at Los Angeles have each loaned me specimens from the collections of their various institutions.

I was the recipient of North Atlantic Treaty Organization Science Studentship 3/60/955 from 1960 to 1963 and the Jeffries Wyman Scholarship at Harvard University during 1960/1961 while I was engaged in this study.

MATERIALS

The material of *Ectosteorhachis* used in this study comes largely from the collections of the Museum of Comparative Zoology and was collected in the "red-beds" of North Central Texas (Wichita Group, Lower Permian). Specimens, including the holotype (American Museum of Natural History [AMNH]

7239), were loaned to me by various institutions as acknowledged above.

Of the genus *Megalichthys*, several specimens in the Museum of Comparative Zoology (MCZ), including material of the North American species *M. macroponta*, were used in this study. However, the majority of the material studied is in the collections of the British Museum (Natural History) (BMNH); this includes the specimen (P. 42516) described by Agassiz (1843) in his definition of the genus (see later for discussion of nomenclature).

ECTOSTEORHACHIS

Dermal skull roof.[1] As is the case in other Rhipidistia, the outer enamel and dentine layers of the dermal bones of the skull of *Ectosteorhachis*, especially in the ethmoid region, tend often to be fused into a single covering in such a way as to obliterate any external indication of the sutures between separate bones (cf. Westoll, 1936). However, in the collections of the Museum of Comparative Zoology, there are many specimens (especially MCZ 6498, 6499, 8652, 8661 and 8668) from which this outer layer has been lost due to the process of weathering of the fossils. It has thus been possible to give a more complete description of the pattern of the dermal bones of the skull of this genus than may be given for many genera of Osteolepidae.

The only published figures of the skull of *Ectosteorhachis* are those of Hussakof (1911), and of Cope and Matthew (1915), but these show few details of the dermal bone pattern.

The premaxillary element in *Ectosteorhachis* corresponds to the bone which in certain other Rhipidistia Jarvik (1942, 1944) has termed a "compound" bone, comprising a true premaxilla, a rostral element which encloses the ethmoid commissure of the lateral line system, and probably also the first of the series of nasal bones. This element has been given the unwieldy name of "naso-rostro-premaxilla." Jarvik (1942, p. 347) believes that the interpretation of such a unit as a "dentigerous rostral" (cf. Westoll, 1936, 1937) is probably incorrect.

The supraorbital lateral line, anterior to the parietal bone ("frontal" of Jarvik), is borne upon a series of four separate

[1] Throughout this paper the terminology used for the various dermal elements in the skull will follow the system of Jarvik (1942, 1944) with the exception of the parietal and postparietal bones which are termed by Jarvik "frontal" and "parietal," respectively.

nasal elements (Fig. 1) which probably represent a reduction from a row of six or seven nasals (cf. *Osteolepis;* Jarvik, 1948) of which the first has been incorporated into the premaxillary unit.

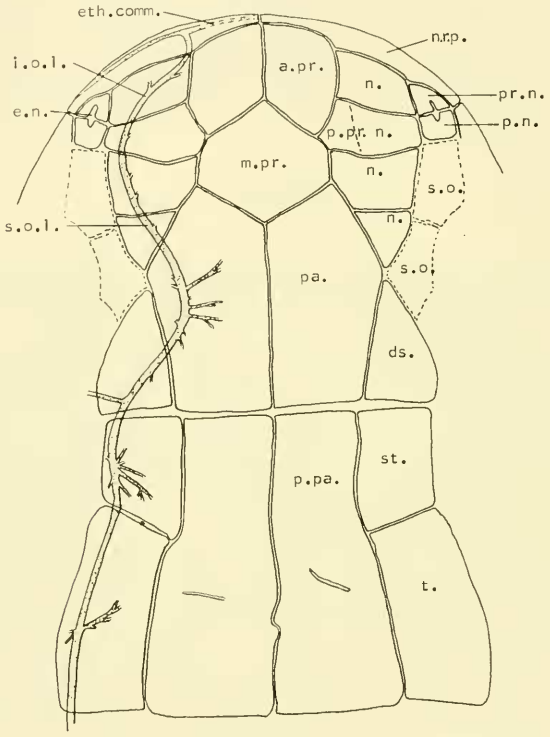

Fig. 1. *Ectosteorhachis.* Diagrammatic reconstruction of the dermal skull roof in dorsal view.

There is a pair of anterior postrostral bones and, posterior to these, a single median postrostral with, in some specimens, a pair of smaller postrostrals lying near its anterior margin, between the median postrostral and the second nasal element.

The infraorbital lateral line is borne upon the lachrymal and thence directly on to the naso-rostro-premaxilla. There are no separate lateral or anterior rostral elements associated with it. The single external narial aperture is bounded by two small bones which have been termed the prenarial and postnarial

(Westoll, 1943). The homology of these bones will be discussed in a later section.

Because of the extent of the postrostral bones, the parietal bones occupy a relatively short part of the roof of the ethmoid region. There is no external parietal foramen. The dermosphenotics, postparietals, supratemporals, and tabulars are arranged in the normal rhipidistian way (Fig. 1). The dorsal margin of the orbit seems to be formed by two supraorbitals on each side (Fig. 1, *s.o.*).

The cheek plate (Fig. 2A). The cheek plate in *Ectosteorhachis* is made up of lachrymal, jugal, postorbital and squamosal bones arranged in the normal rhipidistian manner.

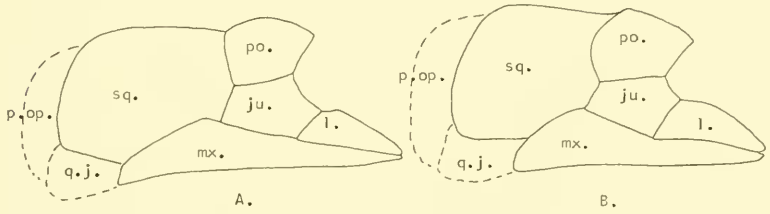

Fig. 2. Schematic reconstruction of the anterior cheek-plate region. A, *Ectosteorhachis*, B, *Megalichthys*.

The palate (Fig. 3A). I have only studied the ethmoid division of the palate. The only other rhipidistian in which the palate has been described in detail is *Eusthenopteron* (Jarvik, 1942, 1944, 1954), a rhizodontid. The palate of *Ectosteorhachis* differs significantly from that of *Eusthenopteron*. The vomers of *Ectosteorhachis* are almost triangular in shape and do not quite meet in the midline. Each vomer bears a pair of alternating tusks and an anterior ridge of marginal teeth. The parasphenoid seems to consist of two parts: the tooth-bearing ridge which reaches about halfway along the flat ventral surface of the endocranium, and a thin bony lamina which (as described by Romer, 1937) continues forward and lateral to the ridge. The whole is fused solidly to the endocranium. The palato-quadrate complex is exactly comparable, as far as I am able to tell, with that described by Watson (1926) in *Megalichthys*.

The conformation of the endocranial part of the palatal aspect of the ethmoid division of the skull is shown in Figure 3A. A major point of interest is the configuration of the anterior

palatal recesses (Fig. 3A, *a.p.r.*). These are shallow pits lying between the anterior margin of the endocranium and the overlying dermal bones; they are separated from each other by posterior medial expansions of the premaxillary bones where each bone bears a stout tusk. When the lower jaws were occluded (as seen in specimen MCZ 9830), these anterior recesses served to receive the tips of a pair of large tusks at the anterior ends of the lower jaw rami (cf. Thomson, 1962).

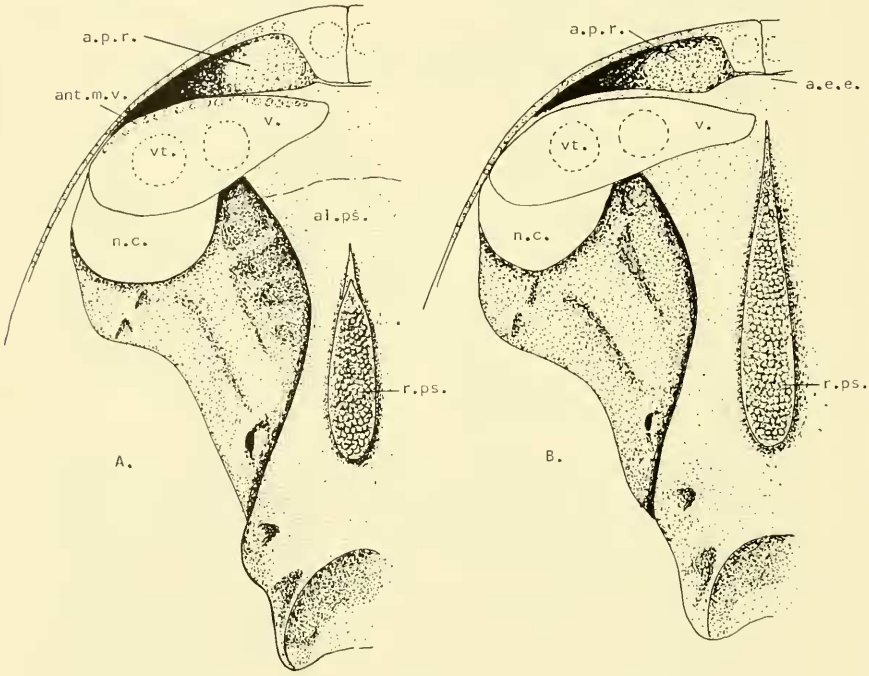

Fig. 3. Ethmoid region of the palate. Ventral view. A, *Ectosteorhachis*, B, *Megalichthys*.

The lower jaws (Fig. 4, A, B, C; based mainly on specimens MCZ 8641, 8826, 8827). As may be seen in Figure 4A, the outer aspect of the lower jaw does not differ greatly from that of *Megalichthys* (as figured by Watson, 1926). It is made up of the dentary and four infradentary elements — splenial, postsplenial, angular, and surangular. These elements are approximately demarked by grooves in the shiny continuous enamel covering on the dermal bones (Fig. 4A, *gr.*).

The inner surface of the lower jaw is made up of the following elements: dentary, three coronoids, prearticular and articular (Fig. 4, B, C). The dentary bone bears, at the anterior tip of the jaw, a large tusk, replaced in an alternating manner (Fig. 4, B, C, *d.t.*), and behind this a broad ridge — which I have termed the *crista dentalis* (Fig. 4, B, C, *cr.d.*). The crista dentalis is covered with small denticles and seemingly serves to occlude with a ridge of teeth on the anterior margin of the vomer. The crista dentalis is formed as an enlargement of the anterior rim of the anterior dentary fossa (Fig. 4B, *a.d.f.*) — a large pit for the reception of the vomerine tusks.

The prearticular covers a large part of the inner surface of the jaw (Fig. 4B, *pr.art.*) and also plays a large role in the formation of the jaw symphysis. A concave facet on each

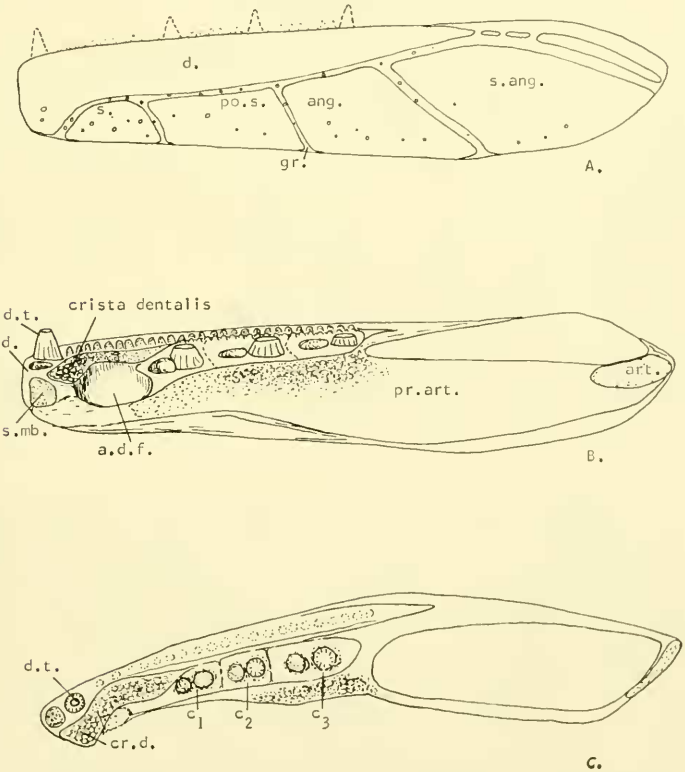

Fig. 4. *Ectosteorhachis.* Lower jaw. A, lateral view of the left ramus. B, inner view of right ramus. C, occlusal view of right ramus.

surface of the symphysial region (Fig. 4B, *s.mb.*) must have contained a small mental bone such as has been described in many Rhipidistia.

The gular series, as depicted by Hussakof (1911, fig. 53), comprises a pair of principal gulars, an anterior median gular, and on each side a row of six lateral gulars.

MEGALICHTHYS

Dermal skull roof. The dermal bones of the skull of *Megalichthys* have been described in part by many authors, but due to the problem of the coalescence of the outer layers of the dermal bones, many details, especially of the ethmoid region of the skull roof, have never been described. Miall (1884), Traquair (1884), Wellbourne (1900), Birks (1914), and Moy-Thomas (1935) have all added in some way to the original description of the skull by Agassiz (1843). Moy-Thomas' figure of the skull (1935, fig. 1) is the most complete restoration. Holmgren and Stensiö (1936, fig. 272 C) figured the anterior region of the snout of a specimen in the British Museum (Natural History), number P. 7875 (not P. 1878 as quoted by Holmgren and Stensiö), a new drawing of which is presented here (Fig. 6E). This specimen shows the arrangement of the dermal bones of the snout very well, since weathering of the fossil has exposed the sutures between the separate bones.

There is some variability in the arrangement of the smaller elements in the snout region of *Megalichthys*. Figure 6 shows the pattern of the dermal bones in six of the specimens (BMNH P. 7729, P. 7842, P. 7846, P. 7878, P. 7886, 21421) which have been used to derive what I consider to be the typical condition (Fig. 5).

The premaxillary unit is a naso-rostro-premaxilla, as in *Ectosteorhachis*. The supraorbital lateral line is carried from the parietal bone to the nasal area of the premaxilla by a row of nasal elements, of which five seems to be the typical number (cf. Pl. 1). Fusions of the nasals may occur (Fig. 6), most commonly between nasals 2 and 3, and nasals 4 and 5.

The most anterior of the nasal elements on each side is a large bone which might be interpreted as being fused with a more median anterior postrostral bone (Fig. 5, *n.pr?*). There is a pair of posterior postrostral bones which may also merge with nearby nasals (Fig. 6F). In certain cases a median posterior

postrostral bone may be present between the posterior postrostrals (Fig. 6F, *m.pr.*).

The infraorbital lateral line passes directly from the lachrymal to the naso-rostro-premaxilla and has no connection with the bones surrounding the external naris. The external naris is bounded by two bones, an anterior prenarial bone which is very large, and a smaller postnarial (Fig. 5, *pr.n.*, *p.n.*).

The parietals are relatively long, compared with *Ectosteorhachis;* they lack the external parietal foramen. With regard to the rest of the dermal skull roof I have been able to add little to Moy-Thomas' description (1935).

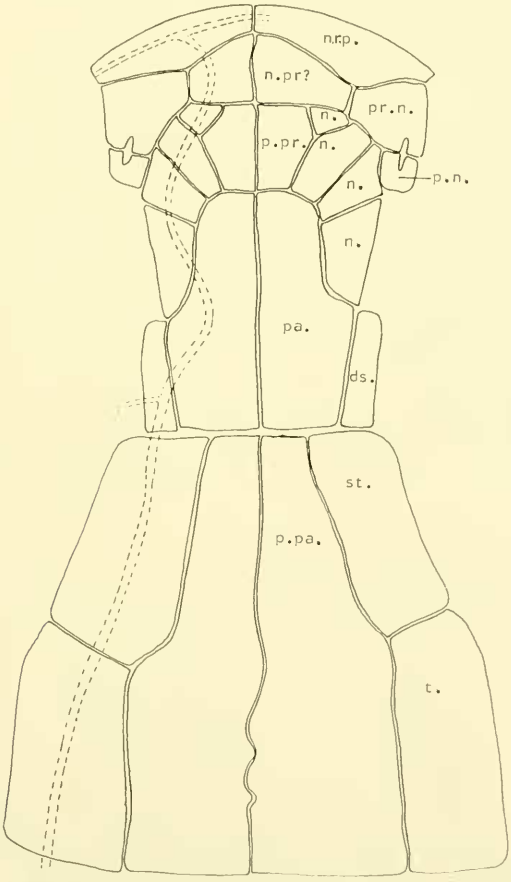

Fig. 5. *Megalichthys.* Diagrammatic reconstruction of the dermal skull roof in dorsal view.

The cheek region (Fig. 2B). The arrangement of the lachrymal, jugal, postorbital and squamosal bones in the cheek region is essentially similar to that of *Ectosteorhachis*.

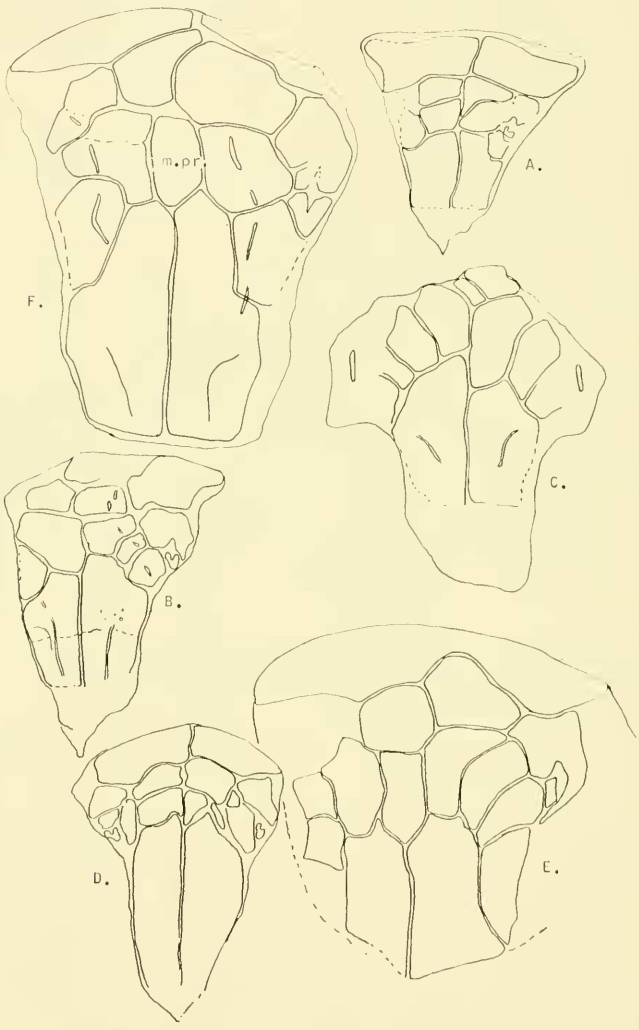

Fig. 6. A - F. *Megalichthys*. Sketches of six specimens showing arrangement of the dermal bones of the ethmoid division of the skull. Dorsal views. A, BMNH P. 7846; B, BMNH P. 7842; C, BMNH P. 7729; D, BMNH 21421; E, BMNH P. 7886; F, BMNH P. 7878.

The palate (Fig. 3B). The ethmoid region of the palate is remarkably similar to that of *Ectosteorhachis.* In *Megalichthys* the anterior palatal recess is also divided into two parts by the bases of the premaxillary tusks, and in addition, by a short anterior projection of the median segment of the anterior margin of the endocranium, which abuts against the premaxillae. (See Fig. 3B, *a.e.c.*)

The tooth-bearing ridge of the parasphenoid is long, reaching almost to the very tip of the endocranium. It has not been possible to establish whether or not there is an anterolateral extension of the parasphenoid corresponding to that of *Ectosteorhachis.* The vomers (Fig. 3B, *v.*) are of roughly triangular shape; they approach each other in the midline in the region of the tip of the parasphenoid. There is a pair of alternating tusks on each vomer; the anterior margin of the vomer is not strongly denticulate.

The lower jaws. The lower jaw of *Megalichthys* was described by Watson (1926, figs. 37, 38); a few very minor modifications must be noted. I have been able to confirm, from specimens (e.g. nos. P. 7886-7888 in the British Museum (Natural History), that there are three coronoid bones in *Megalichthys* (Watson had noted that the posterior of the two coronoids he figured might be double). The adductor fossa is rather wider, and the prearticular bone somewhat more narrow than is shown in Watson's figures. The crista dentalis is absent.

The gular series, as depicted by Moy-Thomas (1935, fig. 3) for example, consists of a pair of principal gulars, an anterior median gular, and six pairs of lateral gulars.

DISCUSSION

There can be no doubt that *Ectosteorhachis* and *Megalichthys* are closely related and have evolved either one from the other or together from the same (Devonian) osteolepid. Bystrov (1950) was of the opinion that *Megalichthys* is a direct descendant of *Osteolepis.* The principal purpose of this study is to set down the diagnostic differences between *Ectosteorhachis* and *Megalichthys,* but in order fully to understand the characteristic features of these fishes it will be necessary to refer to the Osteolepidae of the Devonian.

I have not been able to bring to light any significant differences in the patterns of the dermal bones of the posterior

part of the skull roof between *Ectosteorhachis* and *Megalichthys*, although both differ from the other Osteolepidae in having only two extrascapular bones. There are very characteristic differences between the two genera in the pattern of the dermal bones of the ethmoid region — differences which, incidentally, help to clear up a twenty-year old confusion concerning the homology of the various bones in the narial region.

The composition of the naso-rostro-premaxilla seems to be the same in both *Ectosteorhachis* and *Megalichthys*. The nasal series is essentially the same in both genera; the number of separate nasal elements may be reduced by fusions, but there seem to have been, basically, five nasals, excluding the one incorporated into the premaxillary complex.

The parietal bones in *Megalichthys* are proportionately longer than in *Ectosteorhachis;* this seems to be associated with the corresponding increase in the size of the postrostral elements in the latter genus. The pattern of the postrostral elements seems to have been derived from that of a form such as *Osteolepis* (cf. Fig. 7A) in which there was but a single postrostral element situated between the rear nasals. In *Megalichthys* there is a pair of postrostrals in this position and the anterior nasal bones are enlarged mesially. In *Ectosteorhachis* the anterior nasal bones are small and lie lateral to a pair of anterior postrostrals which have the appearance (cf. Figs. 1 and 5) of having been divided off from the mesial part of the anterior nasals of a form like *Megalichthys*. Posterior to these, in *Ectosteorhachis*, there is a single, median and large posterior postrostral bone corresponding exactly with the single postrostral bone of *Osteolepis* (cf. Figs. 1 and 7A). The arrangements of these bones in *Ectosteorhachis* and *Megalichthys* would seem to indicate that these genera have evolved independently from a Devonian ancestor; however, the judgment of Westoll concerning such bones is that they are anamestic bones and therefore of limited phylogenetic significance.

In order to interpret the significance of the pattern of the bones around the external naris it is necessary to refer to the arrangement of these elements in *Osteolepis* (Fig. 7A), as it has been described by Jarvik (1948). In *Osteolepis* the external naris is bounded ventrally by a single element — the lateral rostral — which is a true rostral element (*sensu* Jarvik), containing a segment of the infraorbital lateral line in its passage from the lachrymal to the premaxilla. The external naris is

bounded by two small dermal bones, sometimes fused into a single element, which are termed the anterior tectals. These three circumnarial bones fit in between the nasal series and the compound premaxilla. Posteriorly they are bounded by the lachrymal, which may slightly underly the lateral rostral, and the supraorbito-tectal, which lies between the posterior of the anterior tectals and the anterior of the two supraorbitals.

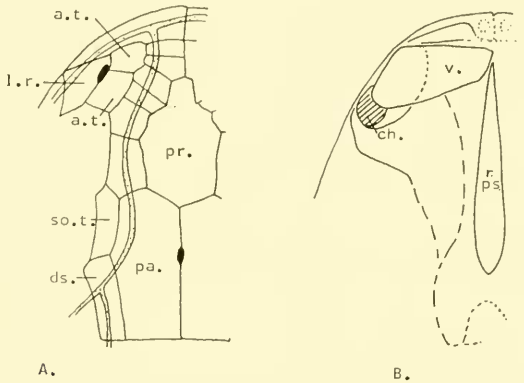

Fig. 7. A, Skull roof of *Osteolepis* (from Jarvik, 1948, fig. 16a). B, Restoration of the ethmoid division of the palate of a Devonian "osteolepid." (Composite of *Osteolepis* and *Glyptopomus*.)

The situation in the post-Devonian Osteolepidae is rather different. In *Megalichthys* the external naris is bounded by two elements — a larger prenarial and a smaller postnarial[1]. As shown in Figure 5, the larger prenarial bone bounds the narial opening in front and it extends both dorsally and ventrally of the naris. There is no connection of this bone with the lateral line system. The postnarial is small and bounds the naris posteriorly. The prenarial is bounded by the nasals, the naso-rostro-premaxilla, the postnarial and the lachrymal. The postnarial is bounded by the nasals, the anterior supraorbito-tectal, the lachrymal and the prenarial. The lachrymal bone makes contact with the premaxilla, and the infraorbital lateral line passes directly between these bones.

[1] It should be noted that Westoll's figures of the snout of *Megalichthys* (1943, fig. 8, c and d), showing prenarial and postnarials of equal size, seem to have been restored after the condition in *Ectosteorhachis*.

In *Ectosteorhachis* the narial aperture is bounded by prenarial and postnarial bones having exactly the same relations to the other bones of the ethmoid region as in *Megalichthys*. The prenarial bone, however, is a small bone of the same size as the postnarial. The small size of the prenarials seems to be compensated for by the large size of the anterior postrostral bones which are not present in *Megalichthys*.

There is some confusion in the literature concerning the homology of these circumnarial elements. Jarvik considers the situation in *Osteolepis* to be primitive and has also concluded from his studies that the lateral rostral bone of this form corresponds to the septomaxilla of the tetrapods (1942). Westoll, on the other hand, has considered the situation in *Megalichthys* and *Ectosteorhachis*, with pre- and postnarial bones, to be primitive. He believes that the postnarial bone, which he states to be typically present in all Rhipidistia (1943, p. 90), is the homologue of the tetrapod septomaxilla. Westoll also considered that the lateral rostral bone of Devonian Osteolepidae and Rhizodontidae did not have a primary relationship with the infraorbital lateral line canal.

All the evidence that I have collected during this study seems to indicate that *Megalichthys* and *Ectosteorhachis* have evolved from typical Devonian Osteolepidae, and the nature of the circumnarial bones serves only to emphasize this view. The position, shape and size of the prenarial bone of *Megalichthys* indicate that this element has been formed from the merging of a lateral rostral and the more anterior member of a pair of anterior tectals of a form such as *Osteolepis*, so that the "new" element encloses the naris from in front. In *Ectosteorhachis* the prenarial is small and we may suppose the decrease in size as compared with *Megalichthys* is associated with a reduction of the anterior tectal component of the prenarial bone. The nature of the prenarial bone in *Ectosteorhachis* may thus be interpreted as evidence suggesting that this genus has been evolved from *Megalichthys* itself.

The postnarial bone in both *Megalichthys* and *Ectosteorhachis* seems to correspond to the more posterior of the anterior tectals of a form such as *Osteolepis*, which, with the shifting forwards of the lateral rostral element, has moved ventrally to enclose the naris from behind.

Although the arrangement of the circumnarial bones in *Megalichthys* and *Ectosteorhachis* may thus be considered to have been secondarily derived from that of Devonian forms,

the name "prenarial" (Westoll, 1943) must be retained for these two genera since it would be inaccurate to consider this element to represent solely the lateral rostral bone. Similarly the name "postnarial" is to be preferred to "anterior tectal" since this bone does not have the same relations with the surrounding bones as it does in the Devonian Osteolepidae.

The supraorbital series was rarely preserved in the material available to me, but seems to have consisted of two elements as in most Rhipidistia (cf. Westoll, 1943).

The cheek region. As shown in Figure 2, the anterior part of the cheek region is essentially the same in both genera. The maxilla and squamosal are slightly longer in *Ectosteorhachis* than in *Megalichthys.*

The palate. The ethmoid division of the palate is very similar in the two genera (see Figure 3). Division of the anterior palatal recess into two portions is effected by an expanded part of the premaxilla on either side of the midline in *Ectosteorhachis.* In *Megalichthys* there is, in addition, a short "buttress" from the anterior part of the endocranium.

The tooth-bearing part of the parasphenoid is much longer in *Megalichthys* than in *Ectosteorhachis.* In the former genus it reaches to the anterior tip of the endocranium and touches the median extremities of the vomers. In *Ectosteorhachis* the tooth-bearing ridge of the parasphenoid ends far posteriorly and there is no contact with the vomers.

The anterior rim of the vomers in *Ectosteorhachis* is more prominently toothed than in *Megalichthys.*

The lower jaws. There is little difference to be observed between the two genera with respect to the outer surface of the lower jaw rami. In *Ectosteorhachis* the grooves in the outer surface of the enamel contain "pit-organs" which are lacking in *Megalichthys.*

With respect to the inner surface of the lower jaw rami, there are greater differences between the two genera. The adductor fossa is longer and a little wider in *Ectosteorhachis* than in *Megalichthys* (in the former the adductor fossa takes up about four-tenths of the total length of the jaw; in *Megalichthys* about three-tenths). The crista dentalis, present in *Ectosteorhachis,* is lacking in *Megalichthys.*

Comparison with other Osteolepidae. We have seen above that the pattern of the dermal bones of the snout of *Ectosteorhachis* and *Megalichthys* (the only non-Devonian members of the family Osteolepidae) may readily be derived from that

of a form such as *Osteolepis;* unfortunately the other Devonian members of this family are less well known (cf. Jarvik, 1948, 1950).

The palate of *Glyptopomus* as revealed in dorsal view only, has been described by Jarvik (1950, fig. 6). By combining details from this description and from specimens of *Osteolepis* in the Museum of Comparative Zoology (nos. MCZ 8737, 5875), I have been able to derive a highly tentative reconstruction of the ventral surface of the palate of an hypothetical generalised Devonian "osteolepid" (Fig. 7B). The vomers are of the roughly triangular shape seen in the later forms, and have a slightly wider region of contact in the midline. The tooth-bearing ridge of the parasphenoid is very long and thin, extending along the whole length of the ethmoid endocranium. It is interesting to note the progressive shortening and broadening of the tooth-bearing ridge in the sequence "Devonian osteolepid" to *Megalichthys* to *Ectosteorhachis.*

The crista dentalis seems to be a specialised feature of *Ectosteorhachis.* The only other genera in which it has been reported are *Panderichthys* (Gross, 1941, fig. 22), which has a few small denticles in this position, and *Litoptychius* (Denison, 1951, fig. 46), which, although it has been described as a rhizodontid[1], may thus have features in common with the Osteolepidae.

CONCLUSIONS

The results of this study have been to show that the Permian rhipidistian of North America known as *Ectosteorhachis* is generically distinct from the Carboniferous genus known as *Megalichthys* which occurs in both Europe and North America. The two genera are very closely related to one another and the evidence of the circumnarial bones in the snout seems to demonstrate that *Megalichthys* evolved from a Devonian osteolepid and that the genus *Ectosteorhachis* separated from *Megalichthys* at a later date. The evidence from the postrostral bones might be interpreted as indicating that the separation between *Megalichthys* and *Ectosteorhachis* occurred before the pattern of

[1]Denison described *Litoptychius* as a member of the family Rhizodontidae, but Orvig (1957) expressed the opinion that it is a member of the Holoptychidae (basing his argument on the structure of the scales). However, the symphysial region of the lower jaw of *Litoptychius* lacks the parasymphysial tooth whorls which are now (Jarvik, 1962) said to be typical of the Holoptychidae and Porolepidae.

these elements had become stabilised; but this is not borne out by the temporal distribution of the fossils. The genus *Megalichthys* occurs in the Carboniferous of both Europe and North America, but *Ectosteorhachis* has only been found in the Lower Permian of North America.

In partial summary of the anatomical evidence discussed in the preceding pages, I present amended generic diagnoses of *Megalichthys* and *Ectosteorhachis*.

Order CROSSOPTERYGII Cope, 1872

Suborder RHIPIDISTIA Cope, 1887

Family OSTEOLEPIDAE Smith-Woodward, 1891

Genus MEGALICHTHYS Agassiz, 1843

Type species: Megalichthys hibberti Agassiz, 1843.

To the list of synonyms given by Smith-Woodward (1891) must be added:

Parabatrachus Owen, 1853: Hay, 1902, p. 362; Berg, 1958, p. 92.

Carlukeus Whitley, 1940, p. 242.

Occurrence: Carboniferous of Europe and North America.

Amended diagnosis (cf. Smith-Woodward, 1891): Dermal bones of the skull arranged as in *Osteolepis* with the following exceptions. The external naris is surrounded by a very large prenarial bone and a smaller postnarial bone. The lateral rostral bone is not present as an independent unit and the infraorbital lateral line canal passes directly from the lachrymal bone to the premaxilla. There are no independent anterior postrostral bones; the posterior postrostral is paired. There is no parietal foramen. There are two extrascapulars. The vomers are triangular in shape and bear two tusks replacing each other alternately. The anterior margin of the vomer is not prominently toothed. The tooth-bearing ridge of the parasphenoid reaches as far anteriorly as to touch the median tips of the vomers. All teeth are rounded in cross-section.

The vertebrae are ossified as narrow rings and the neural and haemal arches are fully developed.

The scales are more or less smooth and punctate. The tail is heterocercal, tending towards diphycercal. The pectoral fins are set rather far back; their bases are covered with scales, as are those of the pelvic fins. The anterior dorsal fin is set slightly

in advance of the pelvic fins and the posterior dorsal fin opposes the anal fin.

Megalichthys hibberti Agassiz, 1843

Lectotype (here selected[1]) : BMNH no. P. 42516. Skull and partial trunk.

Comments: I have no new information to add to Smith-Woodward's diagnosis (1891) of this species.

Genus Ectosteorhachis Cope, 1880

Type species: Ectosteorhachis nitidus Cope, 1880.

Previous authors have thought that this genus is a synonym of the following:

Megalichthys Agassiz, 1843: Cope, 1891, p. 457; Hussakof, 1911, p. 168.

Parabatrachus Owen, 1853: Hay, 1899, p. 788; Hay, 1902, p. 362; Berg, 1958, p. 92.

Occurrence: Lower Permian of North America.

Amended diagnosis (cf. Hussakof, 1911) : Dermal bones of the skull arranged in the manner of *Osteolepis,* with the following exceptions. The naris is surrounded by prenarial and postnarial bones of equal size. There is no separate lateral rostral bone and the infraorbital lateral line passes directly from the lachrymal to the compound premaxilla. There is a pair of anterior postrostral bones and a single, large, median posterior postrostral bone. There are two extrascapulars. The vomers are triangular with a pair of alternating tusks. The anterior margin of the vomer is prominently toothed. The tooth-bearing ridge of the parasphenoid does not reach so far anteriorly as to meet the median tips of the vomers, but ends at the level of the posterior wall of the nasal capsule.

The dentary bone of the lower jaw overlaps the prearticular bone in the symphysial region, as a denticulate ledge — the crista dentalis.

The scales are smooth and punctate. The tail is intermediate between the heterocercal and diphycercal conditions. The pectoral fins are set rather far back. The anterior dorsal fin is inserted in advance of the pelvic fins and the posterior dorsal fin opposes the anal fin.

[1] See below, discussion of nomenclature.

ECTOSTEORHACHIS NITIDUS Cope, 1880

Type: AMNH no. 7239. Skull and anterior scales.

Diagnosis: As for the genus. This is the only known species of *Ectosteorhachis.*

THE NOMENCLATURE OF *MEGALICHTHYS*

The history of the nomenclature of the genus *Megalichthys* is rather complicated. The genus was named by Agassiz in a paper (Hibbert, 1835b) published by Hibbert in 1835[1] for remains of a large "sauroid" fish that had been discovered in the Carboniferous limestone quarry at Burdiehouse near Edinburgh. The remains of this "large fish" had been previously mentioned in various contexts (such as the report of Hibbert to the Geological Section of the British Association for the Advancement of Science, in 1834 [published 1835], and in Agassiz's address to the same meetings). But these instances do not constitute definite "indication" in the sense of the 1961 International Code of Zoological Nomenclature. Hibbert's was the first scientific account and the first proper description.

The remains consisted of some large teeth, some smaller teeth, and scales of assorted sizes. These specimens had been shown, during the 1834 British Association meetings, to Agassiz who was then in Great Britain collecting material for his "Poissons Fossiles." At the time there was a controversy in scientific circles about whether such remains were *sauroid* (i.e. resembling reptiles) or *saurian* (actually pertaining to reptiles). Agassiz and Buckland decided to settle the matter and, subsequently visiting various public museums in England, they found in the Leeds Museum a rather complete head and part of the trunk[2] of a sauroid fish from the Yorkshire coalfields. This, they decided, was identical with the Burdiehouse material. The problem of the *nature* of the Burdiehouse remains was thus solved and ". . . after M. Agassiz had . . . established that these teeth and certain other osseous remains of Burdiehouse belonged to a sauroid fish . . . he considered it as a new genus to which he gave the name of *Megalichthys;* and to the species found at Burdiehouse he added the name of *Megalichthys hibberti.*" (Hibbert, 1835b, p. 202.)

[1] Volume 13 of the Transactions of the Royal Society of Edinburgh, where the paper appeared, was issued between 1834 and 1836. Hibbert's paper (according to Neave, 1940) was published in February 1835. Most authors (e.g. Smith-Woodward, 1891) have given the date as 1836.

[2] Now in the British Museum (Natural History) No. P. 42516.

Fleming in October 1835 described some remains[1] of *Megalichthys hibberti*[2] under the name of *Ichthyolithus clackmanensis.*

In 1837 Sir Philip Grey Egerton, in a revised catalogue of the collections of himself and Lord Cole, uses the name *Holoptychius hibberti* in addition to the name *Megalichthys hibbertii*[3] for specimens in his possession from Burdiehouse. Egerton cites "Agassiz mss" as his authority for the former name. Also in 1837, Buckland uses the names *Holoptychus*[4] and *Megalichthys* and the authority for this, although not stated, was probably also "Agassiz mss" since most of Agassiz's friends in Britain seem to have had access to Agassiz's notes and intentions in advance of publication.

Buckland, however, has confused the picture somewhat: in the text of his work (1837, vol. 1, p. 275) he states that "plate 27, figures 11, 12, 13, 14, represent teeth from . . . the fishes . . . referred by M. Agassiz to a new genus *Megalichthys.*" In the explanation of the plates appearing in volume two of the same work Buckland states that "plate 27, figures 11, 13, 14" are *Holoptychus (sic) hibberti* and "figure 12" is *Megalichthys hibberti* (p. 43). The acknowledged source of the figures is Hibbert's (1835) treatise.

Whatever the reason for this confusion, and regardless of what Buckland actually intended to state, the fact remains that someone, probably Agassiz himself, had recognised that the Burdiehouse remains represented two different fishes. In 1840 Owen made this distinction formal by applying to the larger teeth from Burdiehouse the new generic name *Rhizodus.* But Owen states that the new genus *Rhizodus* is named to replace *Holoptychius hibberti* Agassiz, and presumably, since Owen did not name a type species of *Rhizodus*, he assumed it would simply take over the specific name of "*Holoptychius*" *hibberti* Agassiz. Unfortunately, Owen's authority for the latter name must have been an unpublished Agassiz manuscript for the name does not appear in "Poissons Fossiles" until 1843, when Agassiz merely cites the name, in a list, as "*Holoptychius hibberti* Owen *(Rhizodus)*, Burdiehouse." The specimens concerned are the

[1] Now in the Royal Scottish Museum, Edinburgh, No. 1950.38.58.

[2] "*Megalichthys*" in the sense of this paper.

[3] The spelling of the specific name *hibberti* or *hibbertii* seems to have varied with the preference of the author.

[4] Apparently a misprint for *Holoptychius.*

large teeth and scales from Burdiehouse (figured by Hibbert and Buckland, see Table 1) as well as the specimen figured by Owen (locality unknown).

Agassiz finally (1843) described the "Leeds Head" specimen, as it has become known (and other material which he considered to belong to the species *M. falcatus*), but he did not mention whether or not he still considerd any of the Burdiehouse material to belong to the genus *Megalichthys*. In fact he states only that the localities of *Megalichthys* are numerous, "on en a découvert dans le pays de Galles, dans les environs de Manchester, près de Stafford et dans les environs de Glasgow." This list may by no means be considered complete, since the actual specimen Agassiz was describing came from Yorkshire.

In 1853 Owen described as a new amphibian, *Parabatrachus colei*, a specimen which later (Young, 1868) was shown to be the maxilla of *Megalichthys hibberti* (*sensu* Agassiz).

M'Coy (1855) seems to have been the first to realize the anomaly in the nomenclature of *Rhizodus* and *Megalichthys*. He noted that, in disregard of the facts of the case, the "Leeds head" was considered to be the type of *Megalichthys hibberti* and the Burdiehouse specimens were considered to belong to *Rhizodus hibberti*. M'Coy decided "against my better judgment" to "leave it as it is."

There is little doubt that the name *Megalichthys* was originally intended to describe the "big-fish" of Burdiehouse which is now known as *Rhizodus*. However, there is similarly no doubt that when Hibbert used the name *Megalichthys hibberti* he meant it to apply to the Burdiehouse remains — the "teeth and certain other osseous remains" mentioned above, and these remains, which included both "*Rhizodus*" and "*Megalichthys*" were the true types of *Megalichthys hibberti* Agassiz *in* Hibbert 1835.

Thus Traquair (1884) noted that the Burdiehouse material[1] still remaining in the genus *Megalichthys* has priority concerning the specific name *hibberti*, but, having concluded that the Burdiehouse remains of *Megalichthys* are "different specifically" from the "Leeds head" specimen, and acquiescing to the popular conception that the latter forms the type specimen of *Megalichthys hibberti*, he described the Burdiehouse *Megalichthys* with the aid of new material collected there by Hugh Miller, as the new species *Megalichthys laticeps*.

[1] "Scales and bones . . . actually figured under that name (*M. hibberti*) *along with* (my italics, KST) remains of *Rhizodus* by Dr. Hibbert" (Traquair, 1884, p. 118).

The position taken by M'Coy and Traquair has been accepted by Smith-Woodward in his "Catalogue of Fossil Fishes" and by many subsequent authors (not, however, by all, see Hay, 1902; Jordan, 1923; Berg, 1958).

There seems no merit in proposing that *Rhizodus hibberti* Owen be renamed *Megalichthys hibberti* Agassiz *in* Hibbert 1835; similarly there seems no merit in the proposition that the genus now known as *Megalichthys* Agassiz 1843 be renamed *Parabatrachus* Owen 1853, with type species *clackmanensis* Fleming 1835. The common usage has remained unchanged since at least 1855, and has been adopted by no less authorities than Agassiz himself and Smith-Woodward. I propose, therefore, to invoke Rule 23b of the International Code of Zoological Nomenclature, and formally to request the Commission to stabilise the *status quo* of Smith-Woodward's "Catalogue" (volume 2, 1891) on the subject. I propose that the "Leeds head" (BMNH no. P. 42516) be adopted as the lectotype of *Megalichthys hibberti* Agassiz 1843, and that the large mandibular tooth figured by Hibbert (1835b, pl. 9, fig. 2) now in the Royal Scottish Museum (no. 1950.38.63) be adopted as the lectotype of *Rhizodus hibberti* Owen 1840, in place of the specimen originally figured by Owen and which is now lost.

As a summary of the history of the nomenclature of the Burdiehouse specimens, I have drawn up the following table:

Table 1

The Burdiehouse specimens

All originally described by Hibbert (1835, pl. 8, figs. 1 to 6, pl. 9, figs. 1 to 10, pl. 10, figs. 1 to 3, pl. 11, figs. 2 to 8) as *Megalichthys hibberti* Agassiz.

now known as *Rhizodus*	now known as *Megalichthys*
1. Egerton (1837) from Agassiz MS "*Holoptychius hibberti*"	Egerton (1837) from Agassiz (1835) "*Megalichthys hibbertii*"
2. Buckland (1837, pl. 27, figs. 11, 13, 14, from Hibbert, 1835, pl. 9, figs. 2, 3 and 8) as "*Holoptychus hibberti*"	Buckland (1837, pl. 27, fig. 12 from Hibbert, 1835, pl. 9, fig. 10) as "*Megalichthys hibberti*"
3. Agassiz (1843) as "*Holoptychius hibberti* Owen, *(Rhizodus)*"	Agassiz (1843) as "*Megalichthys*"
4. M'Coy (1855) as "*Rhizodus hibberti*"	M'Coy (1855) as "*Rhizodus hibberti*"
5.	Traquair (1884), actual specimens not cited. Renamed "*Megalichthys laticeps*"
6. Smith-Woodward (1891) lists Hibbert's pl. 8, fig. 1, pl. 9, figs. 2, 3, 9, 10, as "*Rhizodus hibberti*"; Hibbert's pl. 8, fig. 2 as "*Rhizodus ornatus*"	Smith-Woodward (1891) lists Hibbert's pl. 11, figs. 2 to 8, as "*Megalichthys laticeps*"

LITERATURE CITED

AGASSIZ, J. L. R.

1835. On the fossil fishes of Scotland. Rep. Brit. Assoc. Adv. Sci., Edinburgh, **4**: 646-647.

1843. Récherches sur les poissons fossiles. Neuchatel and Soleure, vol. 2, 310 pp.

BERG, L. S.

1958. System der rezenten und fossilen Fischartigen und Fische. Deutscher Verlag, Berlin, 310 pp.

BIRKS, S. G.

1914. *Megalichthys:* a study incorporating the results of work on previously undescribed material. Trans. Nat. Hist. Soc. Northumberland Durham Newcastle, (n.s.) **4**: 307-329.

BUCKLAND, W.

1837. Geology and mineralogy considered with reference to natural theology. 1st ed. London, 2 vols., 552 pp.

BYSTROV, A. P.

1950. Microscopic structure of the bones and teeth of the Carboniferous crossopterygian fish *Megalichthys* (family Osteolepidae). Dokl. Akad. Nauk. U.S.S.R., **34**: 119-121. (In Russian.)

COPE, E. D.

1880. Second contribution to the history of the Vertebrata of the Permian formation of Texas. Proc. Am. Phil. Soc., **19**: 38-58.

1883. Fourth contribution to the history of the Permian formation of Texas. Proc. Am. Phil. Soc., **20**: 628-636.

1891. On the character of some Palaeozoic fishes. Proc. U.S. Nat. Mus., **14**: 447-463.

COPE, E. D. and W. D. MATTHEW

1915. Hitherto unpublished plates of Tertiary Mammalia and Permian Vertebrata. Am. Mus. Nat. Hist., Monograph series, 2.

DENISON, R. H.

1951. Late Devonian fresh-water fishes from the Western United States. Fieldiana, Geology, 11 (5): 221-260.

EGERTON, P. DE M. G.

1837. A systematic and stratigraphic catalogue of the fossil fishes in the cabinets of Lord Cole and Sir Philip Egerton; together with an alphabetical and stratigraphical catalogue of the same species, with reference to their published figures and descriptions. Rev. ed., London, 20 pp.

FLEMING, J.

1835. Notice of the remains of a fish found in connection with a bed of coal at Clackmannan. Edinburgh New Philos. Jour., **19**: 314-316.

GROSS, W.

1941. Über den Unterkiefer einiger devonischer Crossopterygier. Abh. Preuss. Akad. Wiss., math.-nat. Kl., **7**: 1-51.

Hay, O. P.

1899. On some changes in the names, generic and specific, of certain fossil fishes. Amer. Natural., **33:** 783-792.

1902. Bibliography and catalogue of the fossil Vertebrata of North America. Bull. U.S. Geol. Surv., **179:** 1-868.

Hibbert, S.

1835a. On the ossiferous beds contained in the basins of the Forth, the Clyde, and the Tay. Rep. Brit. Assoc. Adv. Sci., Edinburgh, **4:** 642-644.

1835b. On the freshwater limestone of Burdiehouse, in the neighbourhood of Edinburgh, belonging to the Carboniferous group of rocks. With supplementary notes on other freshwater limestones. Trans. Roy. Soc. Edinburgh, **13:** 169-282.

Holmgren, N. and E. A. Stensiö

1936. Kranium und Visceralskelett der Akranier, Cyclostomen und Fische. *In:* L. Bolk, *et alia*, Handbuch der vergleichenden Anatomie der Wirbeltiere, vol. 4: 345-353.

Hussakof, L.

1911. The Permian fishes of North America. Carnegie Institute Publ. no. 146: 153-178.

Jarvik, E.

1942. On the structure of the snout of crossopterygians and lower gnathostomes in general. Zool. Bidrag., **21:** 237-675.

1944. On the dermal bones, sensory canals and pitlines of the skull in *Eusthenopteron foordi* Whiteaves, with some remarks on *E. save-soderberghi* Jarvik. K. Svenska Vetens.-Akad. Handl., (3) **21:** 1-48.

1948. On the morphology and taxonomy of the Middle Devonian osteolepid fishes of Scotland. K. Svenska Vetens.-Akad. Handl., (3) **25:** 1-301.

1950. On some osteolepiform crossopterygians from the Upper Old Red Sandstone of Scotland. K. Svenska Vetens.-Akad. Handl., (4) **2:** 1-35.

1954. On the visceral skeleton in *Eusthenopteron* with a discussion of the palato-quadrate in fishes. K. Svenska Vetens.-Akad. Handl., (4) **5:** 1-104.

1962. Les Porolépiformes et l'origine des urodèles. Colloques Internat. du Centre National de la Récherche Scientifique, Paris, no. 104: 87-101.

Jordan, D. S.

1923. A classification of fishes. Stanford Univ. Publ. Univ. Biol. Sci., **3** (2): 77-243.

M'Coy, F.

1855. Systematic description of the British Palaeozoic fossils. *In:* Sedgwick and M'Coy, The British Palaeozoic Rocks and Fossils. Cambridge, 661 pp.

MIALL, L. C.
1884. On a new specimen of *Megalichthys* from the Yorkshire coal field. Quart. Jour. Geol. Soc. London, **40**: 347-352.

MOY-THOMAS, J. A.
1935. Notes on the types of fossil fishes in the Leeds City Museum. I and II. Acanthodii, Dipnoi, Crossopterygii and Elasmobranchii. Proc. Leeds Lit. Phil. Soc. (Sci. Sect.), **3**: 111-116.

NEAVE, S. A.
1940. Nomenclator Zoologicus. Vol. 3. Zool. Soc. London.

ØRVIG, T.
1957. Remarks on the vertebrate fauna of the lower Upper Devonian of Escuminac Bay, P.Q., Canada, with special reference to the porolepiform crossopterygians. Arkiv. Zool., **10** (6): 367-426.

OWEN, R.
1840-1845. Odontography. London, 2 vols., 655 pp.
1853. Notice of a batrachoid fossil in British coal shale. Quart. Jour. Geol. Soc. London, **9**: 67-70.

ROMER, A. S.
1937. The braincase of the Carboniferous crossopterygian *Megalichthys nitidus*. Bull. Mus. Comp. Zool., **82** (1): 1-67.
1941. Notes on the crossopterygian hyomandibular and braincase. Jour. Morph., **69** (1): 141-160.

SMITH-WOODWARD, A. S.
1891. Catalogue of the fossil fishes in the British Museum. Part 2. London, 567 pp.

THOMSON, K. S.
1962. Rhipidistian classification in relation to the origin of the tetrapods. Breviora, Mus. Comp. Zool., no. 177: 1-12.

TRAQUAIR, R. H.
1884. Remarks on the genus *Megalichthys* Agassiz, with description of a new species. Geol. Mag., (3) **1**: 115-121.

WATSON, D. M. S.
1926. The evolution and origin of the Amphibia. Phil. Trans. Roy. Soc. London, (B) **214**: 169-257.

WELLBOURNE, E. D.
1900. On the genus *Megalichthys* Agassiz, its history, systematic position, and structure. Proc. Yorks. Geol. Soc., **14**: 52-71.

WESTOLL, T. S.
1936. On the structures of the dermal ethmoid shield of *Osteolepis*. Geol. Mag., **73**: 157-170.
1937. On a specimen of *Eusthenopteron* from the Old Red Sandstone of Scotland. Geol. Mag., **74**: 507-524.
1943. The origin of the tetrapods. Biol. Rev., **18**: 78-98.

WHITLEY, G.
1940. The Nomenclator Zoologicus and some new fish names. Austr. Nat., **10**: 241-243.

Young, J.
1868. On the so-called labyrinthodont, *Parabatrachus* (Owen). Trans. Nat. Hist. Soc. Glasgow, (n.s.) **1**: 174-176.

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ABBREVIATIONS USED IN THE ILLUSTRATIONS

a.d.f.	anterior dentary fossa
a.e.e.	anterior extension of the endocranium
ang.	angular
al.ps.	anterior lamina of parasphenoid
ant.m.v.	anterior margin of vomer
a.p.r.	anterior palatal recess
a.pr.	anterior postrostral
art.	articular
a.t.	anterior tectal
c_{1-3}	coronoids
ch.	choana
cr.d.	crista dentalis
d.	dentary
ds.	dermosphenotic
d.t.	dentary tusk
e.n.	external naris
eth.comm.	ethmoid commissure of lateral line system
gr.	groove in surface of lower jaw
i.o.l.	infraorbital lateral line
ju.	jugal
l.	lachrymal
l.r.	lateral rostral
m.pr.	median postrostral
mx.	maxilla
n.	nasal
n.c.	nasal cavity
n.pr?	possible united nasal and postrostral
n.r.p.	naso-rostro-premaxilla
pa.	parietal
p.n.	postnarial
po.	postorbital
p.op.	preopercular
po.s.	postsplenial
p.pa.	postparietal
p.pr.	posterior postrostral
p.pr.n.	posterior postrostral united with nasal
pr.	postrostral
pr. art.	prearticular

pr.n.	prenarial
ps.	parasphenoid
q.j.	quadrato-jugal
r.ps.	median ridge of parasphenoid
s.	splenial
s.ang.	surangular
s.mb.	symphysial mental bone
s.o.	supraorbital
s.o.l.	supraorbital lateral line
so.t.	supraorbito-tectal
sq.	squamosal
st.	supratemporal
t.	tabular
v.	vomer
vt.	vomerine tusk